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Are Temperature and Photoperiod Necessary Cues for Encystment in the Marine Benthic Harpacticoid Copepod *Heteropsyllus nunni* Coull?[1]

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Abstract. *Heteropsyllus nunni* is a marine copepod that builds a cyst and dwells within it during a period of extended diapause. The field abundance of this copepod has been monitored for 10 years, but nothing is known about the cues that induce and terminate encystment. In the laboratory, different photoperiods and temperatures were tested for their effects on encystment and excystment.

The photoperiod and temperature cues tested neither induced nor inhibited encystment in *H. nunni*. Encystment occurred in all treatments, regardless of temperature or photoperiod, suggesting that internal genetic cues, tied to a specific ontogenetic stage, must be the central causal factor. Copepods in the hot treatments encysted and excysted more rapidly than in the cold. Many copepods in the cold treatment encysted (though later than copepods in the hotter treatments), and most were still within the cyst at the end of the 23-week experiment. There were significantly more males within the full cysts than females. A concurrent field study confirmed the known seasonal patterns in the number of encystments relative to the number of free-living forms; *i.e.*, encystment took place in the summer.

Introduction

A state of dormancy or diapause sometime during development is a common adaptation for a myriad of aquatic, terrestrial, and aerial invertebrates. Many of these invertebrates have developed specialized adaptations that protect against periodic (cyclic or acyclic) harsh environmental conditions, such as dry seasons and extreme high or low temperatures. Diapause and quiescence are two such adaptations. Quiescence is characteristically brief, irregular, and controlled by the effective adverse factors. For example, a cold shock might send an invertebrate into a state of quiescence; *i.e.*, the animal enters and remains in a state of torpor until the temperature rises, causing normal physiological functions to resume. Quiescence is reversible, not fixed to a specific ontogenetic instar, and may be induced repeatedly in the same individual (Andrewartha, 1952; Tauber *et al.*, 1986).

In contrast to quiescence, diapause interrupts the normal metabolic program away from its developmental pathway at a specific ontogenetic stage. Moreover, diapause is not controlled by the direct action of sporadic environmental factors; rather it is cued in advance by some predictable cyclic change in the environment (Andrewartha, 1952; Danks, 1987). Diapause is, by definition, neurohormonally driven (Danks, 1987) and involves a more complicated developmental process that commits the organism to a greater metabolic investment (Tauber *et al.*, 1986). As an alternative to the normal developmental pathway, diapause is favored when the expectation of fitness accruing from active growth and reproduction is less than that from survival in diapause (Cohen, 1970).

Insects are the most extensively studied of the diapausing invertebrates (Tauber and Tauber, 1970; Tauber *et al.*, 1986; Danks, 1987). But copepods also exhibit diverse forms of diapause (Elgmork, 1980; Marcus, 1980; Coull and Grant, 1981; Hairston, 1987), the physical manifestation of the process varying with the order. Of the major free-living orders, the largely planktonic Calanoida produce primarily resting eggs (chitin-covered and desiccant-resistant), although some species of *Calanus* and *Neocalanus* diapause in deep waters as a fifth stage (C-V)

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copepodite (Miller *et al.*, 1991). Diapausing eggs are heavier than the subitaneous (immediately hatching) eggs and will sink to the sediment. They are crucial in the reproductive success of these copepods, as an aid in predator avoidance (Hairston, 1987) and as a mechanism for surviving desiccation during drought (Taylor *et al.*, 1990).

In the Cyclopoida, the individual copepod enters into a state of dormancy at the fourth or fifth copepodite stage (C-IV or V); rarely are resting eggs produced (reported only for *Mesocyclops edax*, Wyngaard, 1988). The diapausing cyclopoids sink to the bottom and remain obscured by mud and detrital coverings (Fryer and Smyly, 1954; Elgmork, 1980; Nilssen, 1980).

Diapausing harpacticoids construct and reside in cysts, typically at the adult stage, but diapause is not common in the Harpacticoida. Most encysting species inhabit fresh water and encyst during summer months (Sarvala, 1979; Coull and Grant, 1981; Nalepa, 1985). Indeed, until the discovery of encysted *Heteropsyllus nunni* Coull (Family Cletotidae) in the marine environment, only freshwater species of the family Canthocamptidae were thought to encyst (Coull and Grant, 1981).

Timing for entering diapause is critical and is integrally linked to reproductive success in copepods (Cohen, 1967, 1970; Taylor, 1980; De Stasio, 1990). This timing is most often cued by photoperiod, temperature, or a combination of both. The production of diapausing eggs by calanoids appears to be controlled by the combined effects of photoperiod (Marcus, 1980, 1982a, b) and temperature (Cooley, 1978; Hairston and Olds, 1984; Marcus, 1987); production may also differ with geography (Hairston and Olds, 1984; Marcus, 1987). In cyclopoids, photoperiod is the cue for induction of diapause (Watson and Smallman, 1971a, b; Elgmork and Nilssen, 1978). The dormant cyclopoid C-IV or C-V stages either overwinter or oversummer, depending on the effect of geography on induction (Elgmork, 1955; George, 1973; Cooley, 1978; Elgmork and Langeland, 1980).

Little is known about the environmental cues that initiate diapause in harpacticoids. Sarvala (1979) determined that a particular combination of photoperiod and temperature were needed to induce encystment and excystment in freshwater *Canthocampus staphylinus*. Changes in this light-temperature regime arrested development of the copepodites, inhibited egg production in mature females, and induced the copepods to produce pre-diapause oil droplets. Exposure to low temperature inhibited encystment in *C. staphylinus*.

Heteropsyllus nunni is a recurring member of the intertidal meiobenthos on South Carolina sandflats (Coull and Grant, 1981). The number of free-living animals, relative to encysted ones, has been monitored for 10 years (Coull, unpub.), but little is known about the biology of this animal related to encystment. The objective of this study was to experimentally investigate the effect of the environmental cues, temperature, and photoperiod, (known to induce diapause in other copepods), on timing, sex ratio, ontogenetic stage specificity, and the number of individuals encysting for the marine harpacticoid copepod *Heteropsyllus nunni*.

Materials and Methods

Laboratory environmental cues experiment

Large numbers of *Heteropsyllus nunni* were collected during January and February, 1990, from an intertidal sand flat at Oyster Landing, North Inlet Estuary, South Carolina, USA (33° 19.0′ N, 79° 11.6′ W). At random sites along the exposed sand flat during low tide, the upper two centimeters of sand containing the copepods were scraped up by hand, placed in a bucket with seawater and transported back to the laboratory in Columbia, South Carolina. Live animals were extracted from the sand using a 3% solution of isotonic magnesium chloride. The magnesium chloride solution was added to small amounts of sand, shaken well, and, within 10 min, all living meiofauna in the sand were anesthetized and then decanted. *H. nunni* were separated from other meiofauna under a stereo dissecting microscope and placed in large petri dishes containing filtered artificial seawater (ASW). All copepods were held in an incubator at 18°C, with 16:8 h day:night cycle until sufficient nauplii had hatched. A sand substrate for culture was prepared as follows. Clean sand (300–500 μm size fractions; obtained from the sand flat at Oyster Landing) in a 500 ml flask, was autoclaved, covered with F/2 medium solution (Guillard, 1972), and autoclaved again for 10 min. The sand and medium were then inoculated with 10 mls of *Phaeodactylum tricornutum*. Within a week, *Phaeodactylum* was growing on the sand grains, providing an adequate grazing substrate for *H. nunni*. The culture dishes could then be prepared as follows. The substrate of sand and algae was removed from the flask with a sterile pipet, washed with filtered seawater to remove the excess culture medium and placed in sterile plastic petri dishes with sterile-filtered ASW (salinity 29–30‰). Nauplii were held in 35 × 10 mm size petri dishes, and all other stages were held in 60 × 20 mm size dishes. All experimental dishes with copepods were established during the same day.

The experiments were conducted in two incubators, one set at the ambient winter temperature (10°C) in North Inlet, South Carolina, and one set at the ambient early summer temperature (20°C). Early summer (May, June) is the time of encystment for *H. nunni* in the field (Coull and Grant, 1981). Within these incubators were black boxes within which a long night:short day (15 h dark:9 h light) regime could be simulated in isolation from the other portion of the incubator which was set for long day:

short night (15 h light:9 h dark). Thus, the four treatment conditions were: cold-short day (Cold-SD), cold-long day (Cold-LD), hot-short day (Hot-SD), and hot-long day (Hot-LD).

The black boxes, each with a hinged lid, were constructed of thick (1.85 cm) styrofoam. A slit was cut in the top, and a time-controlled fluorescent light was placed above the slit. The light and box were completely covered with a double layer of black cloth, and cardboard was taped under the upper black box separating it from the lower open light source. We tested the black box for possible light entrance by placing a 35 mm camera containing 400 ASA film in the box and exposing the film using a delayed automatic timer for 6 exposures. The same camera and film were then taken to a photographic darkroom and another six frames were exposed using the same times and settings. There were no differences between the frames exposed within the black box and those in the darkroom, indicating no significant light leakage into the boxes.

Replicate sets of life-history stages (Table I), chosen to represent a wide range of age classes, were exposed to the environmental conditions constituting each experimental treatment. Each ontogenetic stage was isolated in a separate petri dish so that their growth and encystment could be compared. The number of copepods in each dish was determined by the availability of that life-history stage at the beginning of the experiment.

Nauplii, copepodites, or adults obtained from the field might have been pre-cued by their environments to encyst before the initiation of the experiment. To preclude this, gravid females and females with ovaries full of egg masses were used in each treatment so that hatching nauplii would be exposed only to the temperature and photoperiod regime specified by the experimental protocol.

The photoperiod timers in the incubators were coordinated so that daylight would occur in all treatments from 12 noon to 6 pm daily, allowing all feeding, changing of water, observations, and counts to be made during this "daylight on" time. All copepods were fed concentrated drops of the alga *Isochrysis* sp., or additional sand with *P. tricornutum* (as needed). Water was changed at least once a week, more frequently in the smallest dishes. Excess algal clumps, feces, and detritus were removed by pipet weekly. For each dish, weekly counts were made of mortality, the number of full cysts and empty cysts, the stage of development (of nauplii), the number of females with eggs, females with developing eggs in their ovaries, and mating pairs.

The experiment was initiated on March 15, 1990, and was terminated on August 19, 1990; 23 weeks. At the end of the experiment, all of the dishes were removed from the incubators, and 10% formalin with Rose Bengal was added to each dish to preserve all copepods. Every individual was counted and categorized as to life-history stage (nauplii, copepodite, adult, male, female). Each cyst was noted as being full or empty, and, for all full cysts, the copepod was removed, dissected, and sexed.

Table I

*Number of individuals representing each of five life-history stages of copepods (*Heteropsyllus nunni*) placed within each of four experimental treatments*[a]

Stage	No. in dish	Replicate dishes
Nauplii	20	5
Male	5	3
Females (no eggs; full ovaries)	5	3
Gravid females (with eggs attached)	5	3
Post-gravid females[b]	4	3

[a] The experimental treatments are defined in the legends to Table II and Figure 1.

[b] Females removed from isolated dishes that contained nauplii.

Field population study

A field study was conducted on the same intertidal sand flat at Oyster Landing, North Inlet, South Carolina (USA) from which *H. nunni* had been obtained for the laboratory experiments.

Quantitative collections were made by random hand coring with a 2.54 cm diameter core tube in the upper 10 cm of sediment during low tide. Eight samples were taken monthly for one year (Sept. 1988–Aug. 1989). All samples were immediately preserved with 10% buffered Formalin with Rose Bengal added. In the laboratory, copepods were extracted via elutriation where sand was placed in a separation flask and water was gently bubbled up through the sand. This loosened and released the copepods from the sand grains, allowing them to be captured in the outflowing water. Individuals of *H. nunni* were counted, sexed and life-history stage recorded.

Statistical analysis

Free-living and encysted copepod abundance within the four experimental treatments was analyzed separately by the General Linear Model (GLM) procedure (1-way ANOVA, treatment *vs.* final abundance), and Tukey's multiple comparison procedure of SAS to compare treatment effect (SAS Institute, 1985). Data for all of the life-history stage within a treatment were pooled, because the developmental rates of the representatives of each stage were indistinguishable.

Field data on free-living copepods (males and females) and encysted copepods were $\log_{10}(n + 1)$ transformed to meet the assumptions of normality and homoscedasticity. The seasonal abundance of *H. nunni* in the field, by

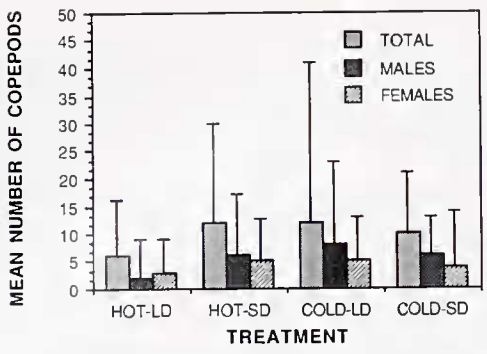

Figure 1. The effect of temperature and photoperiod regimes on the mean number of free-living copepods (*i.e.*, not encysted). The duration of the experiment was 23 weeks. Treatments: Cold, 10°C; Hot, 20°C; LD (long day), 15 h light:9 h dark; SD (short day), 9 h light:15 h dark. Error bars are one standard deviation of mean.

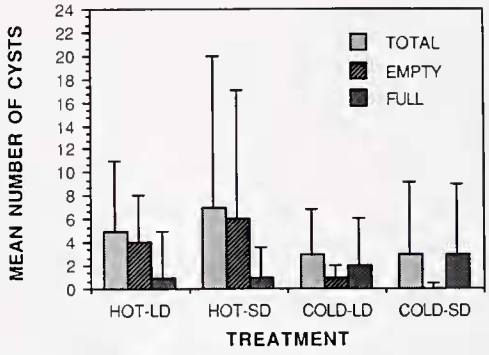

Figure 2. The effect of temperature and photoperiod regimes on the mean number of full and empty cysts. The duration of the experiment was 23 weeks, and treatment conditions are as listed in the legend to Figure 1. Error bars are one standard deviation of mean.

month, as well as the number of females compared to males, were also compared using the GLM procedure (1-way ANOVA, month *vs.* total) and Tukey's multiple comparison procedure. All significance levels were set at alpha < 0.05.

Results

Laboratory environmental cues experiment

A. Free-living Heteropsyllus nunni. The final mean numbers of free-living *H. nunni* in the four experimental treatments were not significantly different ($P = 0.50$; 1-way ANOVA, final number of free-living animals *vs.* treatment). Although the total mean in the Hot-SD treatment was slightly more than double the mean in the Hot-LD (Fig. 1), the great variability within treatment masked any significant difference. There were no significant differences between the number of free-living males compared to free-living females among treatments, again due to high variability within treatment.

B. Encysted H. nunni. Sixteen culture dishes within each treatment represented five different life-history stages. The frequency of encystment events (at least one cyst in a dish) was surprisingly high (69%) in all four treatments. Frequency of encystment events in all dishes (16 total) by treatment was: Hot-SD = 11/16; Hot-LD = 11/16; Cold-SD = 11/16; Cold-LD = 12/16, indicating copepods encysted in most of the five life-history stages originally placed within the dish. The copepods within the cysts were all C-VI, unmated adults that had developed from nauplii in each dish (regardless of the ontogenetic stage placed in the culture dishes). There were no reproductive or post-gravid females, no mated males, and no stages younger than C-VI encysted.

There were significantly more empty cysts compared to full cysts at the end of the experiment ($P = 0.018$) over all four treatments (Fig. 2). Empty cysts in Hot-SD ($\bar{x} = 6.3$), Cold-LD ($\bar{x} = 0.75$), and Cold-SD ($\bar{x} = .37$) conditions were significantly different from each other, but Hot-SD and Hot-LD ($\bar{x} = 3.6$) were not (Tukey's multiple comparison test, $P < 0.05$). There were 48 encystment events in the Cold-LD treatment, 51 in the Cold-SD treatment, 81 in the Hot-LD treatment, and 117 in the Hot-SD treatment, but there was no significant difference ($P = 0.39$) in mean numbers of cysts between treatments (Fig. 2).

The time to first encystment for the Hot treatments was 37 days and 67–77 days for the Cold treatments (Table II); thus, although encystment was delayed in the cold, it was not inhibited. This delay resulted in more cysts with the copepod still inside compared to the Hot treatments, thus, more full cysts than empty cysts at the termination of the experiment (Fig. 2). The number of full cysts among treatments was not significantly different, due, again, to high dish to dish variability.

C. Proportion of males to female H. nunni *in cysts.* There were significantly more ($P = <0.001$) males than

Table II

Time to first encystment for nauplii in four experimental treatments

Treatment*	Begin date	Date 1st encystment observed	Days from nauplii to encystment	No. cysts 1st date observed
Cold-long day	3/15/90	6/1/90	77	3
Cold-short day	3/15/90	5/23/90	67	2
Hot-long day	3/15/90	4/23/90	37	35
Hot-short day	3/15/90	4/23/90	37	9

* Treatment: Cold, 10°C; Hot, 20°C; long day, 15 h light:9 h dark; short day, 9 h light:15 h dark.

Numbers of cysts are totals found on 1st date of encystment. All replicates are combined for each treatment.

females in cysts in all treatments (Fig. 3); mean male/female ratio = 3.5/1.

Field population study

A. Number of free-living H. nunni*/number of cysts over 12 months.* There was a significant difference ($P = <0.001$) between mean copepod abundance by month (Fig. 4). January and February had significantly more free-living *H. nunni* than other months (April–November); March was not significantly different from Jan–Feb or Apr–Nov (Tukey's multiple comparison procedure). Free-living *H. nunni* reached maximum abundance in winter and were low in number, then absent as summer progressed. The mean number of full cysts throughout the year was not significantly different between months, because the number of cysts in the cores was extremely low (Fig. 4). Cysts were most abundant in summer, when free-living *H. nunni* were absent from the core samples (Fig. 4).

B. Free-living males and females over 12-month study. The mean number of males compared to females was significantly different over the one-year sampling period (males and females both with $P = <0.001$) (Fig. 5). The number of males was slightly greater than females in October and November (time of emergence from cysts). The population was dominated by females from December to April, the period of peak egg production (Fig. 5). Free-living males and females disappeared in summer during peak encystment time (May, June, July).

Discussion

In the field, *H. nunni* encysts in early summer (day-length 14 h, temperature 15–18°C). In the laboratory, therefore, we expected *H. nunni* not to encyst under winter (*i.e.*, cold-short day) conditions. Nevertheless, encystment occurred in all treatment conditions and was not inhibited by the dark, cold environment (9 h light at 10°C). Encystment in *H. nunni* must be genetically induced, because sexually immature adults encysted regardless of the surrounding temperature or photoperiod regime. Our results are in direct contrast to those of previous research, which indicate that photoperiod and temperature are necessary mechanisms for inducing copepod diapause, *e.g.*, for calanoids (Marcus, 1980, 1982a, b, 1987; Hairston *et al.*, 1990), cyclopoids (Watson and Smallman, 1971a, b; Elgmork and Nilssen, 1978), and freshwater harpacticoids (Sarvala, 1979). Additionally, no female *H. nunni* dissected from cysts had attached spermatophores, egg sacs, or maturing ova, nor did any males have developing spermatophores. Because mated adults would show at least some of these characteristics, the encysted individuals must not have mated. In *Canthocamptus staphylinus*, however, females with attached spermatophores encyst (Sarvala, 1979), and fertilized, adult females of *Cyclops strenuus* diapause (Naess and Nilssen, 1991).

Although temperature and photoperiod apparently did not specifically cue encystment, they did affect the developmental rates of *H. nunni*. The most significant effect was on nauplii, because naupliar development to adult, and then to encystment, took twice as long in cold treatment (67–77 days) as it did in the hot treatments (37 days) (Table II). In the field, *H. nunni* mate and produce eggs during the winter months. Nauplii hatch from the eggs in late winter or early spring (March, April) when temperatures in the estuary are still quite cool. Therefore, the cold treatments were probably closer to the normal field conditions in temperature and early naupliar devel-

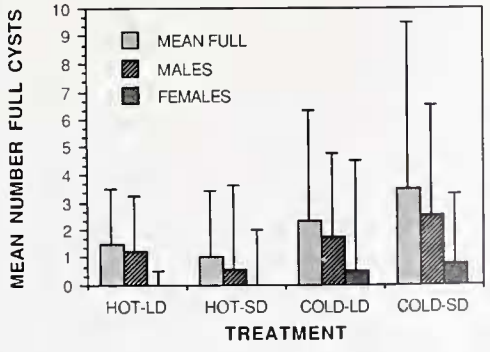

Figure 3. The effect of temperature and photoperiod regimes on the mean number of male compared to female copepods after removal from the full cysts. The duration of the experiment was 23 weeks, and treatment conditions are as listed in the legend to Figure 1. Error bars are one standard deviation of mean.

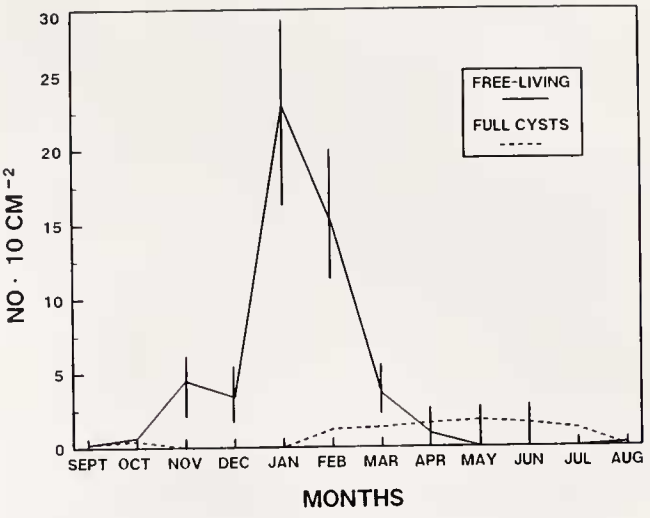

Figure 4. Mean number of encysted and free-living copepods taken from the cores during the field study. Core samples were taken once a month for twelve months. Number per 10 cm^2 is the unit of density for meiobenthos, in contrast to number per m^2 used for macrobenthos. Error bars are one standard deviation of mean.

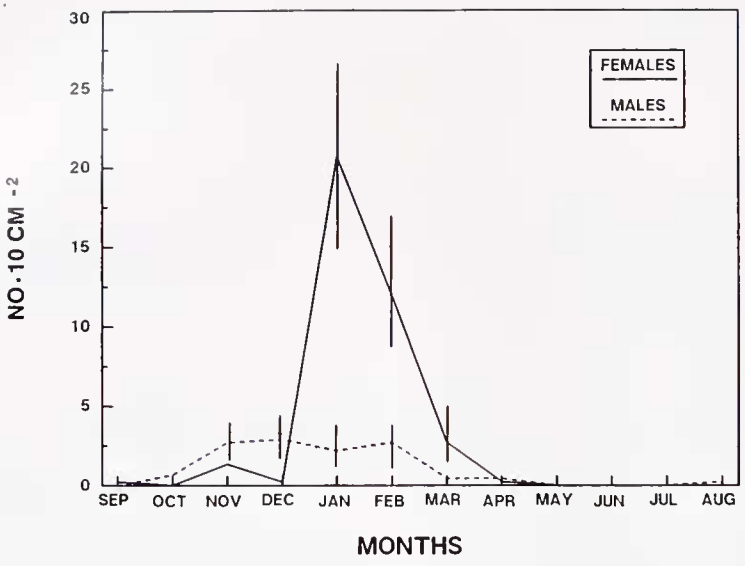

Figure 5. Mean number of free-living male and female copepods taken from the cores during the field study. Core samples were taken once a month for twelve months. Number per 10 cm^2 is the unit of density for meiobenthos, in contrast to number per m^2 used for macrobenthos. Error bars are one standard deviation of mean.

opment than the hot treatment regime. Copepodites normally reach adulthood in early summer (April–May) in the field, and encyst during summer months only (Fig. 4). Greater total number of cysts in the hot treatments (81 Hot-LD, 117 Hot-SD) *versus* the cold treatments (48 Cold-LD, 51 Cold-SD) were probably due to increased rates of development. The high number of encystment events in the hot-short day was unexpected, particularly because longer photoperiod has been implicated as the main cue triggering summer dormancy in other copepods (Watson and Smallman, 1971a, b; Sarvala, 1979).

Not all of the sexually immature adult *H. nunni* encysted. In most treatment dishes there were mating and reproducing free-living copepods throughout the entire 23 weeks, along with encysted individuals; this was unexpected, because no free-living forms have been found in the summer (Coull and Grant, 1981, and Fig. 5). Coull and Grant (1981) hypothesized that the free-living population either moved to another area, or all members encysted. The calanoid copepod *Diaptomus sanguineus* produces diapausing and subitaneous eggs sequentially during the same reproductive period, and Hairston and Munns (1984) suggested that it was using a bet-hedging strategy (*sensu* Stearns, 1976), anticipating that an environmental catastrophe would not occur or would be less severe than expected. Reproductive success could then be insured in either situation. In harpacticoid and cyclopoid copepods, such a bet-hedging strategy is generally not used, because the diapausing stage is not an egg, but an individual (*i.e.*, either copepodite or adult). If the adult is the diapausing organism insuring reproductive success (as opposed to dispersed diapausing eggs), a bet-hedging strategy would not be expected (Hairston, 1987). However, we found free-living harpacticoids along with the encysted ones, as did Cole (1953) and Sarvala (1979). Perhaps these free-living forms are also bet-hedgers, taking the chance that they will not be negatively affected in their non-diapause state. Our inability to find such proposed bet-hedgers in the field (*i.e.*, free-living *H. nunni* in the summer) may be a function of them occurring in very low abundance.

In our laboratory experiment there were consistently more males than females, both in cysts and free-living. These findings are very different from those of Sarvala (1979), who observed that *Canthocamptus staphylinus* males were absent from cysts. However, in the cyclopoid *Cyclops vicinus* and *Thermocyclops crassus*, more males than females emerge from diapause (George, 1973, and Maier, 1989, respectively). The initial data on *H. nunni* (Coull and Grant, 1981) indicated a female to male ratio in the cysts of 2.3:1, but over an 11-year sampling period, the female-to-male ratio for free-living *H. nunni* was 1.6:1 (Coull and Dudley, 1985). Males within cysts outnumbered females by at least 2:1 in the laboratory (Fig. 3). For copepods, a sex ratio other than 1:1 indicates a shift in sexual selection pressure. Male dominance in this experiment may be a laboratory effect, as excessive homozygosity leads to shifting of the sex ratio in favor of males (Hicks and Coull, 1983). An imbalanced ratio could be due to homogeneity of the environment (*i.e.*, small culture dishes), which favors inbreeding, and results in a more homogeneous population. Population density can also

influence sex ratios. Hicks (1984) found that male *Parastenhelia megarostrum* dominated only when the population density was high; in lower densities, females dominated. Another potential influence of gender density is "sexual switching." Hicks and Coull (1983) cite reports of genetic males becoming phenotypic females in response to low population density. In our study, *H. nunni* males dominated over females during Sept–Nov (low density population, 4 per 10 cm^2). In December, the female population increased rapidly from 2 to 23 per 10 cm^2, but the male population remained at previous abundances (Fig. 5). If there were no sex-switching, perhaps this phenomenon was related to developmental differences between males and females.

In certain harpacticoids, males mature much faster than females (Fleeger and Shirley, 1990). Samples taken in early spring had mostly males and copepodites (stages 4–5) and the number of males within the population remained constant; as the copepodites developed, more females appeared, and eventually there were more females than males. Perhaps a similar developmental sequence occurs in *H. nunni,* where males develop, encyst, and excyst earlier than the females, biasing the ratio towards males as the copepods emerge from the cysts. As other individuals mature (females), the ratio then switches to female dominance (Fig. 5).

Biotic factors that induce diapause were not directly tested, but two possibilities exist. Because *H. nunni* cysts are not resistant to desiccation (they collapse around the copepod and dry up when removed from water), perhaps the cyst is used to avoid competition or predation. Where *H. nunni* occurs in South Carolina, the five most abundant copepods (80% of all copepods) have high maximum densities (1056 per 10 cm^2/per) and reproduce from summer through fall (Coull and Dudley, 1985). *Heteropsyllus nunni* reproduces and reaches its maximum population density in winter. In summer months, when other harpacticoids are at their peak, *H. nunni* is within its cyst, dormant. Competition avoidance could possibly be inducing the encystment diapause in *H. nunni.*

Large numbers of juvenile fish that selectively prey on harpacticoid copepods (Ellis and Coull, 1989; Nelson and Coull, 1989) occupy South Carolina estuaries in the spring and summer. A female *H. nunni* carrying eggs is highly visible. The egg sac is large (40+ eggs) and has a bluish tint, and thus *H. nunni* is a susceptible prey item. By reproducing in the winter when there are few juvenile fish, *H. nunni* is less available to predation. As the abundance of juvenile fish increases in the summer, *H. nunni* encysts. *H. nunni* cysts are cryptic (Coull and Grant, 1981) *i.e.,* they are indistinguishable from the surrounding sand. Such camouflage would seem efficient in avoiding visual predators. While there is no field evidence that *H. nunni* is sought as a prey item by young fish, only one fish (*Leiostomus xanthurus*) that consumes mud dwelling harpacticoids has been thoroughly studied from the locale (Feller *et al.,* 1990). Predation avoidance also could be influencing the encystment diapause of *H. nunni.*

We have tested whether temperature and photoperiod (generally important cues for copepod diapause) were significant factors inducing encystment in *H. nunni.* Although cold temperatures slowed development (increasing time to encystment) and hotter temperatures accelerated naupliar development (decreasing time to encystment), photoperiod appeared to have no impact on development or encystment. In the past, perhaps, temperature and photoperiod were important environmental factors cuing these copepods of an impending catastrophe. Now, however, the interactions that induce diapause may be so evolved that the specific catastrophe that favored encystment in the past is obscure. We conclude that for *H. nunni,* the encysted diapause state is a relic adaptive response that has become internalized into a developmental necessity.

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